THE
AMERICAN NATURALIST

VOL. XLVI | March, 1912 | No. 543

PROBLEMS OF EVOLUTION AND PRESENT METHODS OF ATTACKING THEM[1]

PROFESSOR EDWIN G. CONKLIN

PRINCETON UNIVERSITY

THE problems of evolution have been much the same from Darwin's day to this, but the present methods of attacking them are in many respects different from those which prevailed a generation ago. One great problem with which the earlier naturalists were concerned, viz., the fact of evolution, is by common consent, no longer a problem; if it has not been demonstrated that the living world arose through evolution, it has at least been rendered so probable that demonstration could add little to our certainty. And yet we should all like to see the demonstration of evolution on a large scale, such as must have been operative in the past history of living things, but we have little reason to hope that such a demonstration will soon be made.

The enduring problems of evolution concern the means or factors of transmutation. Here also the old method of attack, viz., observation and induction, led to no certainty but only to probabilities of a lower order than those which speak for the truth of evolution. For the past twenty years the futility of the old theories and discussions has been generally recognized, and the desire for more exact knowledge has been keenly felt. Consequently

[1] Introductory address in the annual discussion before the American Society of Naturalists, Princeton, N. J., December 28, 1911.

analytical and experimental work on the problem of the factors of evolution was begun some twenty years ago and has been continued with ever-increasing interest to the present time.

In the first enthusiasm over the experimental method of attack it seemed to many students of this problem that at last a path had been found which would lead straight to the goal, that the causes of all evolution were about to be revealed, and that the practical control of evolution, with all that this implies, was almost within reach. About that time a young physiologist said to the Director of the Zoological Station at Naples, "Why do you spend so much money publishing these beautiful monographs on the Fauna and Flora of the Gulf of Naples?" Dr. Dohrn replied, "You are the first person who has ever asked me such a question; many have asked *how* and *where* I got the money, but no one has asked *why*. What do you mean?" "Only this," said the physiologist, "that within twenty-five years we shall be making experimentally an indefinite number of faunas and floras, and the present one will then be only one of many." In the opinion of many investigators at that time, experimental evolution was soon to give us a new world of living things, and it was about to reveal conclusively the causes of evolution. We have now had one or two decades of this experimental evolution, and it may be worth while to inquire, What has been the net result? If the answer should seem to be somewhat discouraging I would beg to remind you that is so chiefly because the problems have been found to be much greater than was at first supposed. The experimental method as applied to the evolution problem has justified itself; it has set the problem in a clear light and it has brought forth facts of the greatest significance, but it has not enabled man to do in twenty-five years what it took nature twenty-five million years to do.

I

The most significant work on genetics since the time of Darwin is that which is identified with the name of

Mendel. According to the doctrine of Mendel and his followers each organism is composed of a multitude of unit characters, which do not blend nor lose their identity when mixed with others as a result of sexual reproduction, but which may be expected to come out in the end, practically as they went in at the beginning. This conclusion has modified in a striking manner the entire conception of evolution and heredity. We no longer discuss the origin of species, but rather the origin of characters; we no longer rely upon chance to bring out certain hereditary characters, but are enabled at will to make many analyses and syntheses of these characters. These discoveries probably mark the greatest advance ever made in the study of heredity; they have made it probable that evolution proceeds by the evolution of individual characters; but have they shed any light on the method and manner of this evolution? Permutations of Mendelian characters we may have without number, of new combinations of these there may be no end, but, so far as known, no new characters are formed by such temporary combinations, there is no "creative synthesis," no lasting change. Evolution depends upon the appearance of new characters; the discoveries of Mendel show us how to follow old characters through many combinations and through many generations, but they do not show us how new characters arise. These discoveries have given us an invaluable method of sorting and combining hereditary qualities, but Mendelian inheritance, as commonly expounded, does not furnish the materials for evolution.

Many modifications of Mendelian inheritance have been described, many alterations of dominance, or blending of characters, the causes of which are not yet well understood. Perhaps in these "unexplored remainders" may be found the causes of new characters. It is not yet certain that the unit characters, or rather their determiners in the germ, are beyond the reach of environmental influence; it is not certain that in their mixture with others they never combine or influence each other in such manner as to form new unit characters. Indeed, it is difficult

to understand how new characters could ever appear except under one or the other of these conditions. We particularly need at this time more knowledge of the mechanism underlying the gross phenomena of Mendelian inheritance, and then perhaps we may learn under what conditions this mechanism may be altered.

As a result of the work of Mendel and his followers we know much more about heredity than was known before, we have learned how to separate and to combine hereditary characters, we have learned to look for evolution in the appearance of new characters, but we have not learned how to produce new characters.

II

Practically all who have ever thought or written on evolution have found the principal causes of the transmutation of old characters into new ones in the action of extrinsic, or environmental, forces on the organism. As the result of years of labor on this subject Darwin concluded that "variability of every sort is due to changed conditions of life." It is well known that environmental changes produce many kinds of modifications in organisms, and in general these modifications are the more profound the earlier they occur in ontogeny; it is known that slight alterations of the germ cells may produce great modifications of adult structure, and it seems reasonable to suppose that environmental changes of the right sort applied to the germ cells at the right stage would lead to a permanent modification of the substance of heredity and hence to the appearance of new characters of evolutionary value. And yet one of the most striking results of recent work is to show the small effect of environmental changes of all sorts on racial characters. Marked individual modifications may be produced which do not become racial. Usually not one of thousands of variations which occur have any evolutionary value. These variations come with changing environment and with changing environment they disappear. Just as in the individual, so also in the race there seems to be a power

of regulation which causes a return to the type, when once this has been departed from.

In several instances recent investigators have found, or have thought they have found, experimental evidence of the inheritance of characters acquired through environmental changes. But these evidences are by no means conclusive. In a few cases it is known that the effects of changed environment last through two or three generations and then disappear. In such cases racial, or specific, regulation is slow; in most cases this regulation takes place in the first generation after the environmental change disappears. Perhaps in this lingering effect of a changed environment we have the first indication of the appearance and fixation of a new character. Here, undoubtedly, much work of value remains to be done.

Very rarely a sudden variation, or mutation, arises which is perpetuated by heredity and which forms the basis of a new race. In most cases which have been carefully studied such mutations consist in the dropping out of some old character rather than in the addition of a new one, but at least they represent modifications of the hereditary characters, and as such they furnish material for evolution. Whence and how they appear we do not know, for like the kingdom of heaven, they come without observation. Their infrequency, amidst the multitude of somatic variations, indicates the wonderful stability of racial types and teaches respect for Weismann's doctrine of a germplasm, relatively stable, independent and continuous.

This distinction between somatic and germinal variations, between those which concern only the individual and those which are inherited and furnish material for evolution, marks the greatest advance in the study of evolution since the work of Darwin. And just as these germinal variations are the only ones of importance in the process of evolution, so the question of their origin is the greatest evolutionary problem of the present day. How are such germinal variations produced? Do they occur as the result of extrinsic or of intrinsic causes? By

instinct we are all Lamarckians and are inclined to follow Darwin in ascribing variability of every sort, germinal as well as somatic, to changed conditions of life. But this is by no means a necessary conclusion. It is conceivable that germinal variations result from combinations of different germplasms, as Weismann supposed, that the determiners of Mendelian characters do not always preserve their individuality, but sometimes unite in such way as to modify the unit characters; but as yet we have no evidence that new characters are formed in this way, and the study of Mendelian inheritance has made this possibility less probable than it once was. Again it is possible that germinal variations, and new hereditary characters, may result from intrinsic changes in the germplasm, comparable to the spontaneous changes which occur in radium, for instance; such a view of transmutation through intrinsic, spontaneous, changes has points of resemblance to the doctrine of orthogenesis, but of its truth or falsity we have no sufficient evidence.

If changes in the germplasm may be induced by extrinsic conditions, then a real experimental evolution will be possible; if they can not be so induced we can only look on while the evolutionary processes proceed, selecting here and there a product which nature gives us, but unable to initiate or control these processes.

III

Darwin's theory that selection is the most important factor in preserving and building up evolutionary characters remains to this day a theory. The brilliant researches of our distinguished guest, Professor Johannsen, and of our President, Professor Jennings, have shown that the selection of fluctuations, or somatic variations, have no permanent effect in modifying a race; but selection or elimination of germinal variations may be an important factor in evolution, though it has little or nothing to do with the formation of new characters, and serves merely as a sieve, as De Vries has expressed it, to sort the characters which are supplied to it.

On the other hand, selection of favored races and elimination of the unfit is still the only natural explanation of fitness, of adaptation, in organisms. As a species-forming factor selection is probably of less importance than Darwin supposed; as a possible explanation of the wonderful adaptations which all living things exhibit it seems to be all important; but extensive experimental investigations of the causes of adaptation are greatly needed.

IV

The microscopic study of the germ cells during the past twenty-five years—their growth, maturation, union in fertilization, and their subsequent development—has furnished material of the greatest importance for the comprehension of the mechanism of heredity and evolution, and yet almost everything in this field remains to be done. The parts played by the different constituents of the cell in assimilation, regulation and heredity are still in doubt, and in spite of many alluring hypotheses we know practically nothing about the way in which hereditary characteristics arise from the germ. The study of the cellular basis of heredity has to a large extent been guided and influenced by our knowledge of the gross phenomena of heredity, and this must always be the case; but the brilliant discoveries of the last few years as to the cellular basis of sex show the great assistance which the study of cytology may render to the science of genetics. Many interesting experiments have been made upon the germ cells in the attempt to shift dominance, to modify inheritance, to create new characters; in a few instances it has been shown that certain modifications of the embryo or adult organism follow certain modifications of the germ, but in no instance has it been shown that such modifications are inherited and are consequently of evolutionary value.

Not merely the constitution of the germ and the ways in which this may be modified, but also the precise manner in which the structures of the germ become trans-

muted into the structures of the adult are evolutionary problems of the greatest importance. It is an amazing fact that the great problems of ontogeny—*viz.* the underlying causes and mechanism of differentiation—are to-day, after more than a century of scientific observation and experiment, almost as complete a mystery as ever. If we are as yet unable to determine the precise manner in which the structure of the germ evolves into the structure of the adult in the common, ever-present phenomena of reproduction, it is small wonder that we have been unable to determine in detail the way in which one race is transmuted into another.

In conclusion I think it must be admitted that the experimental study of genetics has been a little disappointing. We had supposed that organisms would be more tractable, more willing to evolve, than we find them. The older view that organisms were plastic and could be moulded "while you wait" now reminds one of the view of certain childless theorists, that children are plastic clay in the hands of parents or teachers; both of these views neglect the fact that the living organism, delicate and responsive beyond compare, is still wonderfully strong, stable and stubborn. So far as the factors of evolution are concerned experimental study has thus far been a weeding-out process, and at times it seems that nothing will be left.

The problems of evolution are as much problems today as they ever were, and though some of these problems may soon be solved, we may rest assured that there will always be *the* evolution problem. The path which we thought led straight to the goal has had to be retraced with much labor; the hilltop from which we confidently expected to see the spires of Eldorado has only served to show us how great are the difficulties before us. But this is the order of nature, the common experience of all search for truth, and we would not have it otherwise. "For to travel hopefully is a better thing than to arrive, and the true success is to labor."